A breakdown of size frequency by sex of the two scattergram populations is presented in Figure 7. Here is suggested one reason why more disproportionate pairs are not found: very large males and females are not found in the same populations with very small individuals. Therefore, in addition to the mechanical problems of copulation between *Littorina planaxis* individuals with grossly disproportionate genitalia, there are undoubtedly many ecological pressures involved which keep large and small snails apart in nature, such as size as a factor in withstanding wave shock, desiccation, etc. However, laboratory experiments in which large males were kept isolated with small females, and conversely, for two weeks yielded only one pair, barely exceeding the ⅔ limit, while evenly sized snails under the same environmental conditions paired readily and often.

SEX RATIO

As Figure 7 indicates, there are generally more males than females in the population. A survey of 100 unpaired individuals yielded a ratio of two males to each female: however, when the population as a whole and the large number of snails that are pairing at any one time are considered, the balance between the sexes is seen to be such that there is probably little or no significance in the greater number of males present.

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Macroscopic Algal Foods of *Littorina planaxis* Philippi and *Littorina scutulata* Gould

(Gastropoda : Prosobranchiata)

BY

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The upper littoral periwinkles of the central California coast are often found in association with a number of the higher intertidal macroscopic algae. The studies and observations upon which this paper is based were made on the Monterey Peninsula, on the central California coast, especially at Mussel Point in the vicinity of the Hopkins Marine Station, and at Pescadero Point. The coastline in these areas consists principally of granite boulders and outcroppings interspersed with sandy beaches, heavily overgrown with larger algae through most of the littoral zone. Observations were made during May, 1964, and therefore do not reflect any seasonal fluctuations that might take place.

Despite the fact that both *Littorina planaxis* Philippi, 1847 and *L. scutulata* Gould, 1849 are a conspicuous part of the upper littoral fauna over much of the Pacific coast of North America, almost nothing has been published about them up to now, and while the eastern United States and European periwinkles are generally better known, information on food and feeding patterns is very scarce. North (1954) analyzed size distribution, erosive activities, and gross metabolic efficiency of both *L. planaxis* and *L. scutulata*. Castenholz (1961) used *L. scutulata* as well as *Acmaea* spp. in his studies of grazing effects on diatom populations. From his observations, he assumed "that the primary food of these gastropods is diatom material" (p. 793), with blue-green algae the principal food in the "supra-littoral" fringe. Ricketts & Calvin (1952) state that *L. planaxis* feeds on detritus and microscopic plants scraped from almost bare rock, and that "certain of the rockweeds *(Pelvetia* or *Fucus)* serve the young periwinkles as a sort of nursery, for it is on their fronds and stems that the young will nearly always be found" (p. 20), an observation for which no evidence has been seen during this study. Concerning other species, NEWELL (1958) noted that *L. littorea* ate surface deposits of diatoms and small algae, and also browsed on *Ulva* and *Enteromorpha*.

The answers to three questions were sought in this study. Can these snails eat macroscopic algae? Which algae, if any, are normally part of their diet? How important are these algae in their diets? A number of approaches were used in the attempt to answer these questions. Numerous field observations were made to determine to what algae the snails had access and if they were ever in contact. Principal proof of feeding was based on examinations of the stomach contents of dissected snails, from which ingested tissue fragments could be compared with scrapings from the algae on which the snail was found, or on which it was believed to have fed. In a few cases, feces were also examined for recognizable algal fragments. Several types of laboratory experiments were attempted to supplement field observations. Sometimes it was sufficient to place a winkle together with a dampened piece of alga in a dish. Better results were obtained in an aquarium the contents of which were kept wet, but not submerged, by a fine sea water spray. An aquarium was also rigged to duplicate tidal fluctuations, but conditions were not similar enough to those in the field to get normal responses for any length of time. NORTH (1954) noted that food passed completely through the digestive tract in from 2½ to 6 hours. Thus the stomach contents of any snail kept for six hours with a single type of alga, or starved for six hours and then placed with an alga, could come only from that alga. This seemed to hold true in all cases observed, and provided a simple and reliable check for other types of observations.

A number of difficulties were encountered in the attempt to induce feeding in the laboratory. *Littorina planaxis* has a strong tendency to crawl to the highest part of the dish or aquarium, especially if placed in water. Individuals of both species would frequently cease activity if left undisturbed for more than 6 to 12 hours. Natural conditions, especially with respect to tidal and diurnal fluctuations, proved almost impossible to duplicate, yet it would have been even more difficult to keep track of individual snails in the field or to eliminate unwanted food sources there, especially the ubiquitous "GATGOR" (Green Algae That Grow On Rocks, a term applied to the microscopic flora; work on this aspect of littorine feeding has been done by FOSTER (see below, this issue). Experimental animals had to be run singly in experiments where starvation was a factor because of the tendency of periwinkles to feed on each others' shells. Additional complications resulted from epiphytic algae growing on the test specimens, and from the rapid decay of certain types of algae, especially *Iridophycus*[1] *flaccidum* and *Laminaria Andersonii*, under conditions available in the laboratory.

A number of criteria were set up by which feeding on any particular alga could be substantiated with a satisfactory degree of certainty. At least two of these three standards had to be met before a snail could be considered to have "fed" on the alga in question: (a) the snail was observed on the alga, preferably actively moving and with the radula active; (b) whole pieces or fragments of tissue were found in the stomach or feces exactly matching in cell size, shape, structure, color, type of chloroplasts etc., scrapings or known forms of the alga in question (usually determined by direct comparison); (c) the animal was starved (kept with no signs of feeding or no food) for at least six hours prior to feeding or dissection, and had stomach contents not dissimilar to fragments of the test alga.

Most of the observations of feeding on any one particular alga are based on only a small number of individuals because of the time involved in making a positive determination of feeding, and, in some cases, because such feeding itself may occur only rarely. Some algae are found over only a small part of the range of *Littorina planaxis* or *L. scutulata*, or snails may feed on them only under particularly favorable conditions. It was assumed, however, that positive proof of feeding on an alga, even if based on only one individual, would indicate a species capability of eating or ingesting the alga, if not a preference for it, and that once such a capability was demonstrated, snails observed on such an alga were probably feeding on it.

Littorina planaxis is generally found in the upper regions of the intertidal zone, on "bare" rocks normally moistened only by splash. The height of this region varies considerably with the amount of exposure to surf. *Littorina scutulata* occurs somewhat lower, and in more protected areas, ranging from about +2 feet up to about +6 feet in some areas. It is frequently found in moderate to heavy growths of algae, and very small individuals occur in large numbers in some horizontal *Balanus* beds. The ranges of the two species of *Littorina* overlap considerably in some areas.

Both species are known to depend on microscopic algae (diatoms, greens, and some blue-greens) as a principal food source (CASTENHOLZ, 1961; FOSTER, this issue), especially where macroscopic algae are scarce or absent, as they are over much of the range of *Littorina planaxis*. However, there are areas in which a considerable macro-

[1] Currently placed in *Iridaea*.

scopic algal flora is available, and it is with these areas that this study is primarily concerned. A number of common algae occur in the vicinity of littorine populations, especially *Cladophora trichotoma* (C. A. AGARDH) KÜTZING,[2] *Endocladia muricata* (POSTELS & RUPRECHT) J. G. AGARDH, *Fucus furcatus* C. A. AGARDH, *Gigartina Agardhii* SETCHELL & GARDNER, *Gigartina cristata* (SETCHELL) SETCHELL & GARDNER, *Iridophycus flaccidum* SETCHELL & GARDNER, *Pelvetia fastigiata* (J. G. AGARDH) DETONI, *Porphyra perforata* J. G. AGARDH, *Rhodoglossum affine* (HARVEY) KYLIN, and *Ulva* spp. *Cladophora* is generally found in cracks, crevices, and tidepools, on horizontal surfaces, sometimes together with *Ulva*; *Endocladia, Rhodoglossum,* and the gigartinas are frequently associated together in crevices and on rock surfaces, as well as in scattered individual clusters; *Pelvetia, Fucus,* and *Iridophycus* are commonest on sloping surfaces at slightly lower levels; *Porphyra* often covers the tops of boulders and outcroppings.

One area, in which many of the field observations reported in this study were made, includes all of the above speeics except *Fucus* and in addition has large populations of both *Littorina planaxis* and *L. scutulata.* It is on a granite shelf west of Pescadero Point, at a height of about +4 feet, and was divided for survey purposes into two sections, each of approximately 2 square meters in area. The first is largely horizontal, with a number of crevices up to 10 cm deep and a small tidepool. *Cladophora* is the dominant alga, with some *Endocladia* and *Rhodoglossum* also present; the algae are largely confined to the crevices and the tidepool, the elevated rock areas being bare. The second consists of the vertical west face of the shelf and some of the contiguous horizontal top, about 2 meters from the first area and at the same level. It is almost entirely covered with algae, with *Endocladia, Rhodoglossum, Pelvetia,* and *Gigartina cristata* the most common species, the others present in lesser quantities. One survey showed that the two areas contained 147 *Littorina planaxis* and 329 *L. scutulata.* Surveys were generally made in the morning while the snails were still active from their previous night's wetting, yet had had enough time to feed adequately on the algae.

The feeding behavior of *Littorina planaxis* and *L. scutulata* seems to be a combination of random activity and preferential movement. In the laboratory, snails are frequently observed scraping their radulae along a clean glass surface and have been known to consume considerable quantities of paraffin and powdered carbon. In the field, the stomach contents of snails have revealed large quantities of sand and rock particles, detritus, any number of algal types, and occasional small animals, often still alive and active. There seems, therefore, to be little or no selectivity in what is ingested from any given surface. However, field studies to be discussed later suggest that each species has, at least under some conditions, definite preferences for certain types of substrates or algae.

The radula of these snails seems capable of tearing off quite large pieces of substrate material, and particles of considerable size have been found in their stomachs. Some of the smaller algae such as the filamentous *Cladophora* and the small monostromatous *Prasiola meridionalis* SETCHELL & GARDNER are frequently found almost entire in the stomach of *Littorina planaxis.* The structure of the radula and other mouth parts seems to be similar for both species, and, superficially at least, matches that of *L. littorea* as described by FRETTER & GRAHAM (1962, pp. 26-27).

What the winkles digest of what they take in is still uncertain. Undigested cells and tissue fragments are frequently found in the feces, supporting NORTH (1954) in his conclusion that their digestive efficiency is low, with organic matter assimilation about 7 percent of consumption. Cell wall material seems especially conspicuous, at least in the stomach, and was often useful in identifying the algae on which the snail had fed.

Littorina planaxis does not frequently come into contact with macroscopic algae; most of its range is well above the limits of such algal growth. There are areas, however, where it is found with all of the algae listed previously. In such areas, it shows a decided preference for a rock substrate. (For the purposes of this study the term "rock substrate" includes both microscopic and encrusting algal forms; "algal substrate" refers to macroscopic algae with other than an encrusting thallus; the substrate is the surface to which the snail is attached, and on which, presumably, it is feeding). One survey of the area near Pescadero Point showed only 2% of the *L. planaxis* on algal substrates; for another check under more favorable conditions (overcast sky), about 10% were observed on *Cladophora.* One individual had a considerable quantity of *Cladophora* in its stomach and a filament hanging out of its mouth, so feeding was almost certainly taking place in these cases. *Littorina planaxis* has also been collected on the thalli of what is either a high form of *Rhodoglossum affine* (the name used in this paper), or a juvenile form of *Gigartina cristata.* The stomachs of these snails contained a few fragments of tissue closely resembling scrapings from the alga but in such small quantities as to be an insignificant part of its diet. Snails collected from patches of *Prasiola meridionalis* on rocks covered with bird guano at Mussel Point proved to have large quantities of this alga, often whole thalli, in their stomachs and feces, in addition to quantities of a microscopic chlamydomonad. These are the only instances in the present study in which *L. planaxis* has been found to eat macroscopic algae under natural conditions. A

[2] Nomenclature of algae follows G. M. SMITH, 1944.

number of laboratory experiments suggest reasons for this behavior. In one experiment, thalli of *Endocladia, Rhodoglossum,* and *Porphyra* were finely chopped with a razor blade and spread on the wet bottoms of petri dishes; dishes with whole thalli, and a dish with a growth of "GATGOR" served as controls. A single freshly-collected *L. planaxis* was placed in each dish for 5 hours and then dissected. The snails consumed large quantities of the chopped pieces whole and also the "GATGOR," while the stomachs of the control winkles were empty, even when they were attached to the algae. In an algal preference test run in an aquarium kept damp by spray, the few *L. planaxis* that did not crawl to the top of the tank fed either on rock samples or on soft, decaying pieces of *Iridophycus flaccidum.*

There are several possible reasons why *Littorina planaxis* does not normally eat much macroscopic algae: (a) it is unable to "bite off" pieces of any but the softest or most finely divided algae; (b) it, for some reason, will not crawl on the "unstable" substrates provided by algae: (c) most macroscopic algae are somehow chemically disagreeable to it. Alternative (c) can be safely discarded, since *L. planaxis* showed no aversion to chopped algae. There is at present no evidence for or against reasons (a) and (b), although a brief examination of the mouth and radula showed no obvious differences from those of *L. scutulata,* which feeds much more on macroscopic algae.

In contrast with *Littorina planaxis, L. scutulata* both encounters more macroscopic algae and eats more of it. For instance, in the survey near Pescadero Point cited above, 47% of the *L. scutulata* in both areas were on algal substrates. There were marked preferences for certain species of algae. Of the 153 snails on algae, 72 were on *Cladophora,* 46 on *Pelvetia,* 20 on *Rhodoglossum,* and no more than 5 on any of the other species. Nor is this entirely a reflection of the relative abundance of the algae; *Endocladia,* the most common, had only 3 *L. scutulata* on it, and some of the others had fewer than their relative areas would suggest. Also, observations under more favorable conditions than those reflected in the above survey suggest that all these figures, especially for *Pelvetia,* are at times considerably higher. In other areas, *L. scutulata* is also found on *Fucus* and *Porphyra.* In addition, tidepool populations of *L. scutulata* have been observed scavenging on decaying algae such as *Gigartina corymbifera* and *Prionitus lanceolata* that had been left in the pools by very high tides. The stomachs of snails collected from these algae were stuffed with partially decomposed algal material.

Laboratory studies confirmed that *Littorina scutulata* will readily eat a variety of macroscopic algae. In addition to the *Cladophora* and *Pelvetia* mentioned above in which feeding was definitely observed, snails readily attacked *Ulva,* leaving only tattered shreds. In the preference tank *L. scutulata* was observed on all algae in the tank *(Pelvetia, Cladophora, Gigartina cristata, Endocladia, Rhodoglossum, Porphyra, Ulva, Iridophycus, Laminaria),* and all individuals dissected had macroscopic algal fragments in their stomachs (these were identified in the case of *Porphyra, Laminaria,* and *Ulva).*

The situation therefore seems to be similar to that noted by CASTENHOLZ (1961) for the effects of *Littorina scutulata* on diatom populations; the snails are able to prevent sparse populations from increasing but do not have much effect on well established colonies. The completely bare areas between algal growths in which periwinkles are so frequently found (CASTENHOLZ, *l. c.*) are probably kept bare by continual grazing, and the occasional presence of very young thalli in littorine stomachs supports this. In the study area at Pescadero Point, the *Pelvetia* is worn and indented, and in some places only the stubby remains of thalli can be found in the bottom of cracks, too tightly packed for the snails to reach. Even the *Endocladia* is undercut and trimmed back for about 1 cm above the rock surface in some areas bordering on bare rock. Whether these effects are due to the feeding activity of *Littorina* is not possible to say without lengthy observations and measurements, but considering the quantities of cell material found in stomachs, the depredations observed in the laboratory, and the number of snails involved, the effects of feeding are by no means insignificant. However, well established algal growths seem to hold their own successfully, at least for short periods. Two areas in the field, one with *Porphyra,* the other with *Cladophora* and *Ulva,* were caged with fiberglass netting and ¼ inch mesh galvanized screen into two compartments, one with 25 *L. scutulata,* the other empty as a control (a third compartment with 25 *L. planaxis* was added for the *Ulva, Cladophora* test). After two weeks, no effects were observed that could be directly attributed to the snails, although measurements were not very accurate. The effects on different algae probably vary considerably, judging from the varying quantities of algal material in the stomachs of snails feeding on different plants. *Porphyra* and *Rhodoglossum,* for example, were generally found in much smaller quantities than the softer *Pelvetia* and decaying algae, or the more easily ingested *Cladophora.*

While more work needs to be done on feeding preferences and the mechanisms affecting them, feeding effects, and seasonal and geographical variations in feeding habits, some conclusions can be drawn concerning the macroscopic algal foods of periwinkles. *Littorina planaxis* generally eats only microscopic foods and those macroscopic algae small enough to be consumed entire or nearly so. The reasons for this are not clear, but may be related to the structure of the mouth or the preference for certain types of substrates. *Littorina scutulata* is frequently found eating macroscopic algae, especially *Cladophora, Pelvetia,* and other more easily ingested forms. The effects of this feeding are probably important in limiting the spread of new plants, and the effects on established thalli, while probably considerable in some instances, appear to vary greatly with the species of algae.

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Function of the Cephalic Tentacles in *Littorina planaxis* Philippi

(Gastropoda : Prosobranchiata)

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(10 Text figures)

In Fretter & Graham (1962, p. 14), the following description is given for part of the sensory apparatus in the snail *Littorina littorea:* "Toward its posterior end the head carries a pair of laterally placed tentacles. . . . At the base of each is a cushion-like bulge. . . . This is the eye stalk, and the dark spot on it is the eye. The tentacle, which is tactile and olfactory, is thus the seat of three major senses." The snail *Littorina planaxis* (Philippi, 1847), common along the California coast, has tentacles very similar to those described for *L. littorea.* Studies have revealed that the eye definitely is a light receptor and causes the animal to respond predictably to various light stimuli (Dieter Eckert, personal communication). However, the portion of the tentacle distal to the eye has not undergone extensive investigation, and tactile and olfactory capabilities of this part of the organ are undetermined. In April and May, 1964, studies were carried out at the Hopkins Marine Station of Stanford University, Pacific Grove, California, to determine the behavior and function of that part of the tentacle extending beyond the eye in *L. planaxis.*

The two cephalic tentacles are situated at the sides and slightly back of the large blunt snout. The organs are contractile, and when contracted they fit snugly at the sides of the mouth. Upon extension, they appear as delicate finger-like structures which exhibit movement patterns